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MECHANICS OF DORMANCY IN SEEDS*

WM. CROCKER

INTRODUCTION

Dormancy in plants is common in three organs, seeds, spores, and buds. In this paper I shall limit myself entirely to the discussion of dormancy in seeds for three reasons: far more critical and analytical work has been done on dormancy in seeds than upon the other two organs; obscure correlation effects do not play as prominent a part as in buds; and I am best acquainted with this phase of the subject.

The title of this paper might imply that I am aligning myself with the mechanists as against the vitalists; such is not the case. The vitalists can justly claim that in growth we have as yet explained so little by known chemical and physical laws and have so much till to explain on this basis or on the basis of newly discovered laws that the title "Mechanism of Growth" would imply a very meager discussion of our knowledge of this process. To date we have to discuss growth mainly in physiological rather than mechanistic terms. The situation is rather different with the dormancy of seeds. Here so far as the work is analytical, it indicates that dormancy is brought about by factors inhibitory to general processes preceding or accompanying growth.

In plants of the temperate zone, the seeds generally have a rest period. Howard[1] finds that more than 75 percent of the species, wild and cultivated, growing around Columbia, Missouri, have a distinct period of dormancy. The rest period is more general and much more persistent among wild than cultivated forms. Selection resulting from methods of cultivation have largely disposed of this character in domesticated forms, as is well illustrated by the two closely related species, *Avena fatua* and *A. sativa*.[2] The former is delayed in its germination until the spring following ripening, constituting it one of the bad weeds of Minnesota, the Dakotas and western Canada; while the latter grows rather readily in the late summer and fall and is killed by the severe freezing of winter. When in the eighties the Germans[3] began introducing the wild legumes as forage crops they found one of the great drawbacks was the persistent dormancy of the seeds. Seeds of many plants have a dormancy that persists only until the spring following ripening. Others are carried over two or more winters in the quiescent condition, while still others have the germination of a single crop distributed over the growing seasons of from one to many years.

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* Invitation paper read before the Botanical Society of America and affiliated societies at Columbus, December 29, 1915.

[1] Howard, Mo. Agr. Exp. Sta. Res. Bull. 17.

[2] Criddle, Dept. Agr. Ottawa, Bull. S-7.

The maximum time that seeds can lie in the ground in a dormant but viable condition is a matter of much interest and one that has received considerable attention. Numerous observations[4] of the vegetation appearing upon soil freshly turned up by the digging of wells, ditches, the removal of buildings and the plowing of old meadows and pastures, indicates that various seeds may lie in the soil quiescent and viable for 25 or even 50 years. Peter took samples of soils at various depths from forests that had been grown upon meadow and farm lands for known periods ranging from 20 to 150 years and subjected these soil samples to germinative conditions. The samples from younger forests showed seeds of farm weeds and meadow plants prevalent, while in the older forests there was a gradual displacement by seeds of forest vegetation, and in the oldest forests only the latter appeared. The soil from forests 20 to 46 years old produced 41 species of farm weeds and 35 of meadow plants. In forests over 100 years old he still found *Hypericum humifusum*, *Stellaria media* and *Juncus bufonius*. From his work Peter concludes that seeds of certain plants may lie quiescent in the soil for more than 50 years still capable of germination when supplied proper temperature, light and moisture conditions. Perhaps Ewart has been over severe in his criticism of this rather careful work notwithstanding the possible errors necessarily involved in the method. However this may be, later and conclusive experiments upon buried seeds tend to confirm Peter's conclusions.

Beal[5] has found that out of 22 species representing 16 families, including common plants, mostly weeds, 11 species did not retain their viability after 5 years in the soil, but some seeds of 8 species were still viable after 30 years. It is interesting to note these: *Amaranthus retroflexus*, *Brassica nigra*, *Bursa Bursa-pastoris*, *Lipidum virginicum*, *Oenothera biennis*, *Rumex crispus*, *Setaria glauca*, *Stellaria media*. The appearance of *Stellaria media* in this list is confirmatory of Peter's conclusions.

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[3] Michalowski, Württ. Wochenbl. Landwirtsch. **13**: 175. 1894.

[4] Peter. Nachr. Königl. Ges. Wiss. 673. 1893; 373. 1894.

[5] Beal. Vitality of Seeds Buried in the Soil. Amherst, Mass.

The work of Duvel on the viability of buried seeds, because of the number and range of species represented, the planned duration of the project and the approach to natural conditions, is to be a notable work in this line. He has published[6] the record of earlier tests and he and his co-worker, Mr. Goss, have kindly allowed me to examine the results of the ten-year period. Out of 105 species, representing 25 families, more than half the species, representing more than two-thirds of the families, still show viable seeds ranging from 1 percent in some to nearly 100 percent in others. Of the eight species Beal finds retaining their viability 30 years, the six which are represented in Duvel's list are still viable after ten years; two of them giving about 90 percent germination. Excepting hard forms, seeds of cultivated plants in general show but transient longevity in the soil in contrast to the rather persistent longevity of wild seeds. In general the records on buried seeds confirm the conclusions based on observations and on work of the type of Peter's. In this connection it is interesting to find the claims of the farmers of the South Downs,[7] that *Brassica nigra* seed can lie in the soil for years still capable of growth when supplied proper conditions, confirmed by the exact work of Beal and Duvel.

THEORIES OF LONGEVITY

The question of the nature of the process involved in the gradual loss of viability of seeds with the elapse of time and the effect of conditions upon the rate of this process is of first importance in a discussion of dormancy, for they set the maximum duration of this state. It is well to consider first, seeds that will withstand drying and to consider the loss of viability in approximately air-dry condition. Two explanations capable of experimental investigation have been offered: exhaustion of stored foods and degeneration of the digestive and oxidizing enzymes.[8] Both of these explanations have proved incorrect, for foods and enzymes are present in almost full force for some years after viability is lost.

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[6] Duvel. U. S. Dept. Agr., Bur. Pl. Ind. Bull. 83. 1905.

[7] Kidd. Proc. Roy. Soc. 87B: 408 and 625. 1914.

[8] Crocker and Groves. Proc. Nat. Acad. Sci. 1: 152. 1915. Also unpublished work by the latter.

Ewart[9] says "Longevity . . . depends upon how long the inert proteid molecules into which the living protoplast disintegrates when drying, retain the molecular grouping which permits of their recombination to form the active protoplasmic molecules when the seed is moistened and supplied with oxygen." In this form of statement Ewart's theory is quite beyond experimental investigation. Groves[8] and I have suggested that loss of viability in seeds approaching the air-dry condition is due to the slow denaturing, or coagulation, of certain protoplasmic proteins of the embryo—a statement resembling Ewart's in some ways but one capable of experimental study. The extreme lability of protoplasmic proteins as shown by Lepeschkin[10] would suggest their being denatured far sooner than such proteins as make up or at least are associated in the main with the rather stable oxidizing and digestive enzymes.

The evidence for this hypothesis was gained by studying the relation between temperature and life duration of wheat seeds at temperatures ranging from 50° to 100° C., since this range of temperature gives life durations convenient for experimental purposes.

The following results of this work show the likeness between life duration of wheat grains (*Triticum sativum*) at temperatures above 50° C. and the coagulation time of proteins. At given temperatures the life duration fell with increased water content. When the logarithms of the life duration in minutes was plotted on the abscissae and the temperatures in degrees centigrade on the ordinates a straight-line curve resulted showing that life duration is a logarithmic function of the temperature. The formula applied by Lepeschkin as a time-temperature formula for the coagulation of proteins as well as a temperature-life duration formula for imbibed cells applies also as a temperature-life duration formula for wheat grains ($T = a - b \log Z$, in which T = degrees centigrade, a and b are constants and Z is time in minutes). For rise in temperature the rate of loss of longevity rises much faster than assumed by the van't Hoff law—a law applying rather generally to the rate of chemical reactions *in vitro* as well as to many processes in the living organism. While this law assumes increased speed of two to three fold for a rise of 10° C., wheat containing from 9 to 12 percent moisture showed a coefficient of 7 to 8, and that containing 18 percent moisture 10 to 16 for 10° C. rise in temperature. For life duration of barley seeds, containing considerable moisture, Goodspeed got a coefficient of 10 to 16 and Loeb and Moore on various sea forms found coefficients ranging from 500 to 1,450. It is interesting to compare the above temperature coefficients for life duration with those for the coagulation of various proteins. The latter vary from 6 to 635 according to the range of temperature, moisture content and protein used.

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[9] Ewart. On the Longevity of Seeds. 210 pp. Victoria, Australia, 1908.

[10] Lepeschkin. Ber. Deutsch. Ges. Bot. **30**: 703. 1913.

The evidence is good then that at temperatures above 50° C., with air-dry seeds or those containing somewhat less or considerably more water, the loss of viability is a matter of the denaturing of embryo proteins.

What about loss of viability at laboratory temperatures and temperatures prevalent in natural conditions? When we compare the longevity of wheat, containing 12 percent moisture, as calculated from our measurements at high temperatures either on the basis of the Lepeschkin formula or of the temperature coefficient found, the values are of about the same magnitude as those observed for wheat by White.[11] There is still need of much work on several long-lived and short-lived seeds of which we have fairly reliable records of longevity, to see whether the calculated longevities from measurements at high temperatures by the two methods mentioned above, tally well with observed longevities.

To make concrete the indicated significance of temperature in longevity of seeds let us assume that wheat with a fixed water content at 20° C. has a longevity of 16 years and that the temperature coefficient of 8 still applies at low temperatures. On these assumptions the longevity at 30° C. would be two years, at 10° C. 128 years and at 0° C. 1,024 years.

The total of our results gives considerable grounds for believing that at low and *equable* temperatures and moisture contents medium-lived grains like wheat may retain their vitality several centuries.[12] I am confident, however, that this coagulation theory of longevity has much greater value in opening a line of attack than in matters already established.

The statements above apply to seeds approaching the air-dry condition, but as we shall see later not all seeds lying dormant in the soil for thirty years or more are in this condition. Lepeschkin finds evidence for the presence of a re-dispersal process in fully imbibed plant cells. At ordinary temperatures he believes this increases many fold the life duration of plant cells. It and many other factors such as change in reaction of the cell may modify the speed of coagulation. Here too it is possible that carbon dioxide or other narcotics produce a state of rigor thereby greatly lengthening the life of the seed as is indicated by the work of Kidd. It is possible that seeds like *Amaranthus retroflexus* and *Brassica nigra*, lying in the soil for thirty years or more nearly or quite saturated with water, entirely consume their stored food in respiration and die of starvation. It is not known whether these seeds remain alive longer in this condition or in air-dry storage.

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[11] White. Proc. Roy. Soc. London 81B: 417. 1909.

[12] It is probable that the action of oxygen as well as noxious gases must be avoided. Becquerel. Ann. Sci. Nat. Bot. IX 5: 193. 1907.

The changes involved in the rapid loss of vitality by seeds that will not withstand drying are still more obscure. The nature of the injury produced by drying is also entirely unknown.

Causes of Dormancy

In securing delayed germination of seeds, plants are not limited to the dead monotony of one method. As one studies the problem more fully he wonders whether there is any conceivable method of securing delay not made use of in one plant or another. I believe that failure to grasp the variety of methods and the counter attempts to explain all delays by one or at most two methods, is the main source of the controversy, error and confusion that have prevailed in this field.

We will now consider two general topics: (1) Methods of securing dormancy and (2) methods of overcoming it, or the action of forcing agents upon dormant seeds. The two topics are far from distinct. Certain subheads under either topic could be shifted to the other without violence, thus constituting an extremely complex interrelation between the general topics and the subheads under them. The classification here offered is for the convenience of discussion and must be subject to change with growth of knowledge in the field. Nevertheless, I believe some such classification very desirable at this time in clearing up a chaotic situation and in giving future experimentation direction and aim.

METHODS OF SECURING DORMANCY

As to the mechanism by which delay in germination of mature seeds is secured when they are placed under ordinary germinative conditions, we will consider the following: (1) Rudimentary embryos that must mature before germination can begin; (2) complete inhibition of water absorption; (3) mechanical resistance to the expansion of the embryo and seed contents by enclosing structures; (4) encasing structures interfering with oxygen absorption by the embryo and perhaps carbon dioxide elimination from it, resulting in the limitation of the processes dependent upon these; (5) a state of dormancy in the embryo itself or some organ of it, in consequence of which it is unable to grow when naked and supplied with all ordinary germinative conditions; (6) combinations of two or more of these; (7) assumption of secondary dormancy.

Primary Dormancy.—(1) It has been shown that at ripening many seeds have immature embryos[13] that must complete their development before germination can begin. Such embryos vary from an undifferentiated group of cells or perhaps in some cases a fertilized egg to mature embryos. A considerable range of immaturity often appears in a single species. This seed character appears more or less distributed through all the large groups of seed plants as is shown by a few illustrations: Gymnosperms—*Ginkgo biloba*, *Gnetum Gnemon;* Dicots—*Eranthis hiemalis*, *Ranunculus Ficaria*, *Corydalis cava*, *Stylidium*, *Gagea arvensis;* Monocots—*Hymenocallis speciosa*, *Paris quadrifolia*, *Erythronium denscanis.* The maturing of the embryo in some of the seeds of this class requires weeks and even months in the germinator, and delays germination to that extent. The immature embryos of this group must not be confused with those of certain saprophytes and parasites that germinate in the immature condition.

2. So-called hard seeds have coats that entirely prevent absorption of water. This phenomenon predominates in the Leguminosae but it is also common in Cistaceae and Malvaceae[9, 14] and has been observed in perhaps a dozen other families. In some species all the seeds of the crop are hard but more frequently only a portion. In either case in nature the germination of a single crop is distributed over a considerable period, probably in some cases amounting to many years. For instance, Nobbe found that red clover seeds placed in water do not

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[13] Goebel. Organographie der Pflanzen, 454. Jena, 1898–1901.

[14] Guppy. Studies in Seeds and Fruits, 585. London, 1912.

all swell at once, but a few at a time, a considerable percent remaining hard and viable even after a decade.[15] Hard seeds become permeable very slowly under dry storage, more rapidly in germinators under laboratory conditions, and apparently still more rapidly under widely fluctuating natural conditions. The means by which this resistance to water absorption is secured has been mainly studied in the legumes. Here a controversy has arisen as to whether it is due to the cuticle or to the "light zone" of modified cellulose of the palisade layer. Perhaps there is more evidence in favor of the former for small and medium sized seeds, and for the light zone or deeper layers of the palisade cells in larger seeds. Either will explain the rather general efficiency of surface abrasion or carbonization as means of forcing.[9, 14] Verschaffelt[16] has lately given this controversy an interesting turn. He finds that seeds of legumes in general have open micropyles that give free access to the water absorbing tissues below and that in addition in the subfamilies Caesalpinioideae and Mimosoideae rifts or lacunae communicating with water absorbing tissues below are present over much of the seed surface. Water fails to enter because it will not wet the walls of these openings. It will enter, however, if the seed is first soaked for an hour in ethyl alcohol and then placed in water. The alcohol readily enters the openings and furnishes a path for the inward diffusion of water. The efficiency of alcohol as a forcing agent varies much with different legumes, showing slight or no effect in many. It is likely Verschaffelt's explanation applies to a portion only of the legumes and perhaps not at all to other hard seeds. Moreover Ewart finds that in some hard seeds all layers of the integument are highly impervious to water and Guppy claims this is prevalent among hard-coated forms with large seeds. There is need here of much more investigation, especially of non-leguminous seeds.

For cultivated legumes Hiltner[17] claims that crops ripening in dry climates or in dry periods show a larger percent of hard seeds. On the other hand Harrington[18] finds that alfalfas and clovers, generally, grown on a variety of soils and ripening under most diverse climatic conditions, have about 90 percent of hard seeds if hulled by hand, but generally less than 20 percent if hulled by machine. The huller thus acts as a rather effective abrasive agent and the study of the machine hulled seeds concerning hardness throws more light upon the effectiveness of the machine than upon the seeds themselves.

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[15] Nobbe. See 17.

[16] Verschaffelt. Rec. Trav. Bot., Neerland. 9: 401. 1912.

[17] Hiltner. Land. Forst. Wirtsch. Kais. Gesundh. 3: 1. 1902.

[18] Harrington. U. S. Dept. Agr. Farmers' Bull. 676.

Concerning the biological significance of hard coats it may be stated that they place a family of seeds, otherwise extremely susceptible to injurious agents among those of the greatest longevity. Applying the principles mentioned in our coagulation conception of life duration, such seeds in the soil have ideal conditions for longevity —low equable temperature and moisture content. Moreover the impervious coats protect them against other organisms and the slow action of oxygen.

3. In the light of Müller's[19] recent work it is not strange that some seeds are held in a dormant state because the force of the expanding contents is not sufficient to rupture the coats. He found that in various seeds that germinate readily the outward pressure of the contents at the time of rupture was but slightly greater than the breaking strength of the water-saturated coat. Both lay in the region of 3 to 4 atmospheres. It has been shown that the breaking strength of filter paper, leather, Laminaria thallus and most other organic materials of colloidal nature rises or falls with a fall or rise in water content. Müller found the same true of seed coats. In the cases studied the breaking strength of the dry coats was several times the expanding force of the enlarging seed contents.

Of seeds inhibited in their germination by this method, *Alisma plantago*[20] and *Amaranthus retroflexus*[21] have been most fully studied. Water impervious coats play no rôle here for both absorb water very rapidly and reach saturation after about 5 hours' soaking. In the saturated condition it is estimated that the embryo of *Alisma plantago* due to imbibitional or osmotic absorption of water is exerting an outward pressure on the coats of about 100 atmospheres. In *Amaranthus retroflexus* the outward pressure is probably much less, but in both seeds the gel-like coats are considerably stretched, and the embryo rapidly extends beyond the bounds of the coat as soon as the latter breaks. Any time after maturity naked embryos of both these seeds are capable of immediate growth, showing no dormant period. The embryo of Alisma is a rather slow grower but that of Amaranthus very rapid. The latter shows a growth elongation of several hundred percent after 12 hours in the germinator under optimum conditions.

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[19] Müller. Jahrb. Wiss. Bot. **54**: 529. 1914.

[20] Crocker and Davis. Bot. Gaz. **58**: 285. 1914.

[21] ——— ——— Unpublished work.

The intact seeds of both these species are dormant when harvested. *Alisma plantago* remains so for years unless acted upon by some of the agents mentioned below, but Amaranthus in great part loses its dormancy after 2 or 3 months of dry storage. This "so-called" after-ripening in Amaranthus seems to involve hysteretic changes in the colloids of the coats by which they fall in elasticity or breaking strength. This hysteretic effect will be discussed under secondary dormancy.

Certain temperature relations of after-ripening in Amaranthus are of great interest. Temperatures above 40° C. will produce some germination in the ripe seeds harvested from green plants, and the minimum temperature falls as after-ripening progresses. Even fully after-ripened seeds have their minimum temperature lowered by removal of coat restrictions. As is true of gels, generally, the viscosity of gels of the coats lowers with rise of temperature and with it the breaking strength falls. The combined action of the hysteretical changes of the coat with this temperature effect on their breaking strength seems to explain the minimum temperature changes accompanying after-ripening.

Any treatments that greatly weaken the coats without injury to the embryos are good forcing agents for the dormant seeds of both Alisma and Amaranthus. Abrasion by various means, carbonizing with sulfuric acid or treatment with a great range in concentration of acids under proper adjustment of time are effective in Amaranthus. In addition bases are good forcing agents for Alisma as well as Sagittaria. The place and method of action of acids and bases as forcing agents have been variously interpreted. Fischer[22] found that the seeds of Sagittaria and some other water plants, which normally lie for years in water in a dormant stage, are readily forced by acids and bases. He believed that rapidly diffusing hydrogen and hydroxyl ions produce differences in potential thus arousing the dormant embryo.

It has since been shown that the embryos are not dormant and that the action is mainly upon the rather consistent gels of the coats leading to a mechanical weakening of these. This mechanical weakening is probably brought about by two means. As for gels quite generally acids and bases increase water absorption and thus lower the breaking strength in accordance with the law mentioned above. The coats consist of pectic or other materials rather readily hydrolyzed or otherwise decomposed by acids and bases and are mechanically weakened by such chemical transformations.

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[22] Fischer. Ber. Deutsch. Bot. Ges. **15**: 108. 1907.

Fischer found that the transfer of seeds of many water plants to foul water, in which abundant growth of bacteria and fungi occurred on the coats, aroused them from dormancy. He attributes the effect to acids or bases produced by the organism and acting upon the embryo. I am convinced that the rather slight forcing effect of organisms is due to enzymatic hydrolysis or decomposition of the coats and not to the acids or bases produced. In Alisma concentrations of acids, sufficient to give but slight forcing action, are too high to permit considerable growth of the embryo; and in Scirpus and Sparganium[21] no concentration of acid or base will force germination. We should except sulfuric acid (sp. gr. 1.84) which acts as a carbonizing agent and produces good germination of the former after nearly 3 hours' treatment but only abnormal germination in the latter after more than 24 hours' treatment. As we shall see later there is a well-established case in which the forcing action of the acid is upon the embryo. This is claimed as the point of action in light stimulated seeds where acids rather generally have the power of substituting for light, but this claim is entirely without critical evidence. In *Amaranthus retroflexus*, a light inhibited seed, the acid has its effect upon the coat. There is need of a critical study of the effect of acids on light sensitive seeds to learn what part of the seed is affected as well as the specific nature of the effect in each case.

As we have already mentioned, seeds of *Amaranthus retroflexus* may lie in moist soil for thirty or more years in a viable dormant condition. It is well to mention known and needed investigation that may aid in elucidating this phenomenon, for the findings for Amaranthus probably apply in a general way to seeds of black mustard, shepherd's purse, Lepidium and many others, that lie in the soil for years in a state of quiescence with the embryo partially or fully saturated with water. As aids to keeping the seeds of Amaranthus in a dormant condition in the soil there is the extra resistance to expansion offered by the soil and the power of these seeds to take on secondary dormancy, a matter discussed later. Such seeds are laid open to exhaustion of their foods by leaching and respiration. As is coming to be found the case for many seeds the coats of Amaranthus have a most efficient semi-permeable membrane. This is well shown by the fact that they can lie in a saturated solution of copper sulfate or $4N$ sodium chloride for weeks without marked injury. Examination will show whether leaching is further prevented by stored foods being held in the condensed condition. A thorough study of respiratory rate under conditions of temperature and moisture approaching those of soil dormancy will give an idea of food loss from this source and with leaching losses will indicate whether the longevity of these seeds in nature is determined by starvation. Life duration experiments such as Groves and I have conducted upon wheat may offer evidence as to whether these seeds will persist longer in dry storage or whether some process similar to Lepeschkin's postulated redispersal theory increases their longevity in the imbibed condition.

4. Of the seeds that are delayed in germination by seed or fruit coats reducing the oxygen supply below the minimum for germination, various species of Xanthium have [3] been most thoroughly studied. The character appears in both the upper and lower seeds of the bur but is more marked in the former. The seeds grow readily when the testas are removed. Increased oxygen pressure or hydrogen peroxide induce germination of the intact seeds. Under normal oxygen pressure high temperature acts as a forcing agent. This gives the odd phenomenon of two temperature minima for germination—one with coats removed and a much higher one with coats intact. In nature the lower seed generally germinates the year after ripening and the upper the following year. This regularity is often broken up by agencies that modify the testa or by high temperatures during the first summer.

Shull[24] in published articles and Denny in unpublished work have done much to clear up the mechanics of the behavior of Xanthium seeds toward oxygen. The naked embryos absorb much more oxygen from the air than embryos in the testas. Embryos in intact seeds show an increase in oxygen absorption with increase in the partial oxygen pressure of the atmosphere. *These facts establish the important point of increased consumption of oxygen under oxygen supplies favoring germination.* The naked embryos of both seeds have rather definite oxygen pressure minima for germination; this is considerably higher for the upper than for the lower seed and it falls for both as the temperature rises. *These facts explain in part both the differences in behavior*

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[23] Crocker. Bot. Gaz. **42**: 265. 1906.

[24] Shull. Bot. Gaz. **52**: 453. 1911.

of the two seeds with the coats intact and the forcing action of high temperatures.[25] As time elapses, either in dry storage or in natural conditions, the coats become more permeable to oxygen; also the rate of oxygen absorption by the naked embryos falls. *These facts explain in part the timing of the delay in nature and the greater efficiency of increased oxygen pressure as a forcing agent at mid-winter than immediately after ripening.* In nature, however, frosts and many other conditions modify the testas; also the embryo may have its oxygen minimum lowered by sugar accumulation. For the latter, however, we have no evidence.

Upon the whole the mechanics of the dormancy and of its duration is fairly well elucidated for the seeds of the cocklebur.

Since the discovery of this method of delay in Xanthium, many other seeds, especially composites[26] and grasses, [27, 28] have been found to possess similar characters. It has been found that in unafter-ripened seeds of *Chloris ciliata* high temperature forces germination even in normal oxygen pressure as it does in the intact seeds of cocklebur; while the unafter-ripened seeds of wild oats, *Avena fatua*, and "rain barley" (barley ripening during rainy weather) germinate in normal oxygen pressure only at relatively low temperatures. As after-ripening progresses the minimum temperature falls in the first and the maximum rises in the last two. In *Chloris ciliata* light and certain salts will substitute for increased oxygen pressure. No experiments have been performed to elucidate most of these phenomena. It is not known for instance whether the vicarious action of light and salts upon Chloris is due to effects upon the coat increasing its permeability to oxygen, or upon the embryo, lowering its minimum oxygen pressure for germination as high temperature apparently does in the cocklebur. The disposition of the workers to philosophize rather than to outline and perform searching experiments has proved a great hindrance to progress.

It has been shown that the presence of glucose[29] may substitute for oxygen in the growth of certain plant organs as well as in the germination of seeds. It is possible that the amount of sugar present in seeds of the type now under discussion may determine their ability to germinate in limited oxygen supply and that agencies like light and salts act indirectly through sugar formation or carbohydrate hydrolysis. This and other possibilities need careful experimental study in this connection.

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[25] It is possible that permeability changes in the testa may also be induced by temperature changes.

[26] Becker. Inaug. Diss. Münster. 1911.

[27] Gassner. Jahrb. Ham. Wiss. Anstalten Beih. 1. **29**: 1911.

[28] Atwood. Bot. Gaz. **57**: 386. 1914.

[29] Lehmann. Jahrb. Wiss. Bot. **49**: 61. 1911.

Matters are made more difficult here by the fact that we do not know the exact method by which oxygen acts in determining growth and growth rate of organs of seed plants. Nabokich[30] gives it a multiple rôle. Directly, it stimulates growth as do salts and other substances. This function can be cared for by various other reagents. Next, it oxidizes what would otherwise be fatal products of anaerobic respiration and thereby makes continued life possible. Finally, he probably would not deny that indirectly at least it is important in releasing necessary energy for growth through normal respiration.

In connection with germination Becker[26] speaks of oxygen as having a catalytic function and Lehmann[31] connects it with the hydrolysis of proteins, thus furnishing substances necessary for the growth of the embryo. The assumptions of these authors are in great need of experimental evidence; they have such difficulties to meet as the facts that there is greatly increased oxygen consumption under increased oxygen pressure and that hydrolysis of proteins is extensive in certain seeds in oxygen-free[32] germinators. Kidd[7] finds that the narcotic concentration of carbon dioxide decreases with decreased oxygen pressure and believes that oxygen supply in seeds of the type under discussion operates indirectly through the anaesthetic action of carbon dioxide. Shull[33] is inclined to think that in the cocklebur the effect of oxygen is through increased respiration, for here the oxygen consumption increases greatly with increased partial pressure and with coat removal.

The unsolved problems here are among the most difficult and fundamental of those met in growth.[34]

Dude[35] finds that imbibed seeds *in vacuo* are soon killed by accumulation of toxic materials of intramolecular respiration. Of the five species studied the life duration in this condition ranged from about

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[30] Nabokich. Beih. Bot. Centralbl. **26**: 7. 1910.

[31] Lehmann. Biochem. Zeitschr. **50**: 388. 1913.

[32] Godlewski. Bull. Acad. Sci. Cracovie. **9**: 705. 1912.

[33] Shull. Bot. Gaz. **57**: 64. 1914.

[34] Höber. Phys. Chem. Zelle. u. Gewebe. 752–780. Berlin, 1914.

[35] Dude. Flora **92**: 203. 1903.

15 to 50 days. Mazé[36] found that seeds retain their vitality but a short time even under the considerable reduction in oxygen supply involved in water storage. Besides injury from toxic products of intramolecular respiration he found leaching of stored foods very extensive in some cases.

In the light of these facts the question occurs, Why is it that many seeds can have their germination inhibited by a sub-minimal oxygen supply without suffering from toxic products of partial anaerobic respiration? To answer this question we need a thorough study of the products of anaerobic and partial anaerobic respiration in cocklebur and other seeds of similar behavior.

In this connection we should also remember that seeds of various water plants[20] will withstand storage under water for years and with removal of coat restrictions will germinate fairly rapidly and grow rather extensively in total absence of oxygen. In these seeds anaerobic respiration apparently produces little if any poisonous products.

Shull[37] has observed that seeds of a number of wild forms, including both water and land plants, will withstand at least 4½ years' storage in water. The discrepancy between these results and those of Mazé is probably best explained by the fact that Shull was working with the seeds of wild plants while Mazé was dealing with cultivated species. A student in this field is impressed by the fact that through cultivation seeds have largely lost those characters that make for long dormancy and in general for success in the struggle under natural conditions.

Characters we have already pointed out for various seeds of wild plants will largely explain the findings of Shull. Hard coats, restricted swelling, partial anaerobic respiration that does not produce toxic materials, and perhaps finally the disposition of certain seeds to keep stored foods in the condensed rather than in the hydrolyzed condition, are all found in one seed or another showing dormancy and all reduce the rate of food exhaustion and tend to maintain a healthy condition of the embryo.

5. Turning to the fifth general method by which dormancy in seeds is secured, we find a situation not met in the previous classes: the embryo or a part of it fails to grow when naked and supplied with all the external conditions necessary for germination. It must go through a series of changes or after-ripen before germination can

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[36] Mazé. Ann. Ins. Pasteur, **14**: 350. 1900.

[37] Shull. Pl. World, **17**: 329. 1914.

occur. Of the seeds of this class *Crataegus mollis* has been most fully studied. Both the optimum conditions[38] for after-ripening and much of the nature of the changes[39] involved, have been worked out.

After-ripening occurs most rapidly at 5° C., but the structures surrounding the embryo influence greatly the rate of the process at this temperature—with the naked embryo 3 or 4 weeks are required, with the testa only intact 3 or 4 months, with both testa and stony carpel intact more than a year. Investigations indicate that the coats retard the after-ripening at least in large part by limiting the oxygen and water supply to the embryo. The possibility is not excluded, however, that they hold in some inhibiting substances.

Regarding the changes involved in the after-ripening of the seed Eckerson finds that in the dormant condition the hypocotyl is slightly basic or neutral to phenolphthalein, while the cotyledons, capable of immediate growth, are quite acid. As after-ripening progresses the hypocotyl becomes more and more acid. The acid reaction of the hypocotyl seems to produce general physical-chemical conditions favorable for water absorption, enzyme formation and action, and, through these, for growth. In accord with this certain acids greatly hasten after-ripening. Apple seeds behave qualitatively as Crataegus, but quantitatively the dormancy is much less persistent.

A study of several more representatives of this physiological type of seed is needed in order to know how generally the findings for the haw hold for the group.

There is no doubt that every one of the five types of dormancy we have described is represented by many different seeds. It is also likely that combinations of two or more types of these show up in a given seed. While in general the embryos are primarily responsible for the dormancy in the first and fifth types and the coats for the second, third and fourth types, every one shows a more or less complex interaction between the coats and the embryos.

Secondary Dormancy.—It is a rather generally observed fact that some seeds capable of immediate germination can be thrown into a secondary dormancy by a period in a germinator lacking some one condition necessary for germination or involving a substance inhibiting germination or one hardening the colloids of the coats. A few cases may be cited. Gassner[27] produced dormancy in the light requiring seeds of *Chloris ciliata* by a period at 20° C. in a dark germinator; Kinzel[40] in the dark requiring seeds of *Nigella sativa* by a period in an illuminated chamber at 20° C.; Crocker and Harrington[41] in Johnson grass (*Sorghum halepense* L.) and Davis and Crocker[21] in *Amaranthus retroflexus* by a time in the germinator at subminimal temperatures; Kidd in white mustard by exposure of imbibed seeds to sufficient partial pressure of carbon dioxide and Crocker and Davis[20] in the acid treated seeds of *Alisma plantago* by treatment with almost any concentration of copper sulfate. In all these cases except Nigella the authors find that the modification is in the seed coats and that the embryos are at no time dormant. This interpretation for Nigella accords with the known facts quite as well as Kinzel's interpretation. Except for Nigella, on which experiments relative to this point have not been made, removal or rupture of the coats gives immediate and vigorous germination and in white mustard drying produces the same effect.

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[38] Davis and Rose. Bot. Gaz. 54: 49. 1912.

[39] Eckerson. Bot. Gaz. 55: 286. 1913.

Some evidence has been gained regarding the nature of the changes involved in dormancy production, but there is need of much more work on this point. In some cases it involves such simple reversible processes as the stoppage of free gaseous exchange by the filling of capillary spaces with water.[42] In other cases pectic or other gel-like materials fill the spaces.[43] In *Alisma plantago* the copper ions harden the coat colloids, increasing their breaking strength and rendering impossible the further osmotic and imbibitional swelling of the embryo. In white mustard Kidd believes the carbon dioxide lowers the permeability of the coat to gases, thus hindering the free elimination of carbon dioxide and absorption of oxygen. The carbon dioxide narcotizes the embryo and the reduced oxygen supply is important in lowering the amount of carbon dioxide necessary for narcosis. Kidd[7] has shown that the carbon dioxide content of soils is sometimes sufficient to induce dormancy in white mustard. This factor is, therefore, operative in natural conditions. It is probably limited in its significance to relatively few seeds, for many seeds (cabbage, onion, barley, beans, and peas) cannot be thrown into dormancy by any partial pressure of carbon dioxide.

In *Amaranthus retroflexus*[21] I believe dormancy production is the counterpart of after-ripening and involves partially reversible changes in the colloids of the seed coats in which hysteresis is important. Hysteresis is very common in colloids and involves the lagging of certain secondary changes behind the primary change that causes them. In *Amaranthus retroflexus* seeds, a month or more of dry storage is necessary for after-ripening. The after-ripening seems to consist merely in a lowering of the elasticity and breaking strength of the colloids of the coats, rendering the force of the expanding contents capable of rupturing them. On the basis of data we need not cite here I interpret after-ripening and dormancy production in these seeds as follows. Upon drying, the colloids of the coats slowly take on new characters which lag a month or more behind the drying and give them much lower elasticity and breaking strength when again soaked up. *This is after-ripening.* When soaked up the coats do not immediately take on that character stipulated by high water content; but if the seeds, in a state of saturation, are prevented from breaking the coats, the old strength is gradually attained and dormancy secured. It is possible that Kidd in white mustard was dealing with hysteretic changes involving permeability characters and that carbon dioxide was acting merely as an inhibitor to germination allowing these time changes to occur rather than acting directly upon the coats as he thinks. Undoubtedly other changes in the coat of non-reversible type are sometimes involved in producing dormancy.

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[40] Kinzel. Ber. Deutsch. Bot. Ges. **25**: 269. 1907.

[41] Unpublished Work at the Seed Laboratory of U. S. Department of Agriculture.

[42] Haberlandt. Bot. Jhrb. **3**: 857, 1875.

[43] Windisch. Wochenschrift Brauerei, **22**: 89. 1905.

While in the cases of induced dormancy, cited above the main change is in the coats, these changes act in every case through some character of the embryo or other seed or fruit organs—the force with which they expand, their capacity to be narcotized by carbon dioxide, etc. Conditions inducing dormancy by coat changes must simultaneously bring about important changes in the seed contents; such as hydrolysis and condensation of stored foods and enzyme formations. These, however, play no rôle or only a minor rôle in dormancy induction. Finally it is likely that lasting dormancy may be induced in which the significant changes are in the embryo. Indeed this is assumed to be the general situation by certain workers who are unduly imbued with a certain type of ultravitalism that prevents a thorough physical and chemical analysis of the problem.

The biological significance of this secondarily induced dormancy is clear. It throws many seeds into a condition of quiescence in nature from which they may be aroused only by a marked change in conditions on one hand or a slow process of decay of the coats themselves on the other. This gives seeds ready for germination at every break in vegetation—a matter of great importance in the struggle among plants. Induction of dormancy in seeds capable of germination also throws much light upon a phenomenon very common in nature—the primary dormancy taken on by seeds of non-viviparous plants with the approach of ripening. As Guppy and Kidd have emphasized, vivipary is generally connected with absence of seed coats or with poorly developed ones. Well-developed coats play a dominant part in primary as well as in secondary dormancy; on the other hand we have already shown that primary dormancy is sometimes due in the main to the embryo and is only lengthened by the coats.

Forcing Agents

The effect of forcing agents upon dormant seeds is a topic deserving much attention, but time will compel us to limit it to a few general statements. Already a number of references have been made to certain forcing agents.

Acids and bases are frequently found effective through a physical or chemical modification of the colloids of the coats, while in the haw acids apparently force germination by changing the reaction of the embryo.

Freezing or freezing and thawing[44, 45] are means of forcing and probably are of very great significance in nature. In general the work in this line has not been directed at the mechanism involved and throws little light upon the part of the seed effectively modified as well as the nature of the modification. Low temperature, but not freezing or freezing and thawing, hastens the after-ripening in the embryo of Crataegus. Evidence indicates, however, that the beneficial effects of freezing are often through coat changes.

The forcing action of salts[27, 31] is frequently reported, but here again the studies are not directed at the mechanism involved, although many writers make the gratuitous assumption that their effects are nutritive or stimulative to the embryo. They will have to meet the rather general existence of non-living semi-permeable coat membranes that permit little or no entrance of salts. It may be found that salts are often effective through a modification of the colloids of seed coats.

[44] Kinzel. Frost und Licht als beeinflussende Kräfte bei der Samenkeimung. Ulmer, Stuttgart, 1913.

[45] Pammel and Lummis. Proc. Soc. Prom. Agr. Sci. **24**: 89. 1903.

Soil as a substratum[27, 31, 48] frequently forces the germination of dormant seeds. It also produces secondary dormancy. Here a number of reagents may play a part, each acting either upon the coat or upon living structures: changed oxygen supply, salts, acids, bases, and other substances. Kidd has shown that mustard seeds are thrown into secondary dormancy by the high carbon dioxide content of certain soils. Other narcotizing and inhibiting substances may also be present in the soil.

High temperature[23] is frequently effective. In some cases it acts through coat restrictions to oxygen or water absorption. These restrictions give a germinative temperature minimum far above that of the naked embryo. Independent of coat restrictions, however, the minimum temperature for the germination of seeds of many wild forms is very high, being near 20° C. This embryo character accentuated by coats plays a very great rôle in dormancy in nature. Alternation of temperatures[27, 46] is also an effective means of forcing many seeds. It is extensively used for practical testing in the seed laboratory of the U. S. Bureau of Plant Industry. The method of action of alternating temperatures is not known.

Finally light[46] is an important condition in determining dormancy: it forces the germination of many seeds that would otherwise be dormant and inhibits many that would grow in darkness, while the greater number of seeds are indifferent to it. In certain seeds Kinzel has connected the effect of light with mobilization of reserved materials while Lehmann and Ottenwälder[48, 49] on the basis of inferential and philosophical considerations give it a rôle in protein hydrolysis. The assumption that it is always effective through modification of living substances alone is quite gratuitous. It may modify either the living structures or the coats, each in a variety of ways. It must be recognized that the latter are in the more exposed position. There is great need of a scrutinizing chemical-physical study of the effect of light upon seed germination.

We must point out a biologically significant matter concerning light requiring seeds: in the soil they lack this one condition for germination and are held in a dormant state. Some seeds (Nicotiana

[46] Pickholz. Zeitschr. Land. Versuchs Oesterr. **14**: 124. 1811.

[47] Lehmann and Ottenwälder. Zeitschr. Bot. **5**: 337. 1913.

[48] Ottenwälder. Zeitschr. Bot. **6**: 785. 1914.

and others), belonging to this class, hold their vitality for years in the soil.[49]

While we are discussing light as a forcing agent, let us revert to certain points in the classification we have used in this paper. The question may justly be raised, Why not classify lack of light as one of the methods of securing dormancy in seeds, just as was done for oxygen, rather than treat it as a forcing agent? This question must be answered by repeating that the two general topics are closely interrelated and that while the present classification has virtue in convenience of discussion and in giving aim to future research it must be subject to modification with advance in knowledge. Again free oxygen is generally spoken of as an essential condition for growth of organs of flowering plants while light is generally merely a formative condition and only indirectly necessary through food supply. True, later work has somewhat modified the clearness of this distinction. Free oxygen is not necessary for considerable growth in seeds of various water plants and can be vicariously displaced by other conditions for limited growth in certain organs of other flowering plants. Even if its main function in maintaining continuous growth is the oxidation of toxic products of intramolecular respiration, it stands in a much more immediate essential relation to growth than does light. Moreover we do not know how general and immediate a relation oxygen holds to continuous growth through supply of necessary energy by normal respiration nor how generally its so-called stimulative effects can be temporarily displaced by other conditions. For light-sensitive seeds, light has been found capable of displacement in one after another until very recently the most persistent case, seeds of Gesneriaceae,[50] have yielded to experimentation. I am much inclined to believe that future investigation will show that light acts through the elimination of one of the other five dormancy producing factors mentioned above rather than in such a fundamental and essential relation as oxygen.

SUMMARY

In closing let us consider a few of the more important general bearings of the facts treated in this paper.

1. Dormancy in seeds results generally from the inhibition of one

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[49] Duvel and Goss. Unpublished Work on buried seeds referred to in the Introduction.

[50] Gassner. Zeitschr. Bot. 9: 609. 1915.

or more of the processes preceding or accompanying germination. The problems are becoming questions of the conditions for growth of the embryo and the fundamental changes occurring in the embryo with the beginnings of germination on one hand: and a study of the physical characters (permeability and breaking strength) of the colloids of the seed coats as affected by aging, various conditions and reagents, upon the other.

2. Seed coats have a surprisingly important rôle to play in both primary and secondary dormancy. Often they are of such colloidal nature as to be modified by even very low concentrations of a variety of reagents thus permitting the growth of the embryo. In the past such results have been interpreted frequently and wrongly as stimulus responses.

3. Regarding conditions for germination of seeds, the recent trend is toward the need of certain general physical conditions and away from the need of specific chemical stimuli, or even chemical stimuli at all. The same change in view is occurring in reference to germination of pollen.[51, 52] We apparently have here a generalized physiology in contrast to the situation in the organs of more highly differentiated organisms. In mammals for instance dormancy of an organ as well as its rate and course of development are often determined by specific substances from the great number of highly specialized glands. Even if Kidd's conclusion is correct, that carbon dioxide often produces dormancy by narcotizing seeds, we have the action of a general product of metabolism rather than a specific material.

4. After-ripening of seeds, or the changes occurring during dormancy and finally making germination possible, may involve growth of a rudimentary embryo, fundamental chemical changes in an otherwise mature embryo, or chemical changes in the coats. In after-ripening there is often a complex interrelation between coat and embryo changes.

5. Problems in dormancy lend themselves beautifully to the mechanistic attack.

6. Finally, I must state that the dominantly mechanistic interpretation I have given dormancy in seeds is not that held by all or perhaps even a majority of the workers in this field; but this viewpoint has recently made great advances possible and promises much for the future.

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[51] Tokugawa. Journ. Coll. Sci. Tokyo, 35: 1. 1914.

[52] Martin. Bot. Gaz. 56: 112. 1913.